Taxonomy and phylogeny of brown-rot fungi in the *Antrodia* complex (Polyporales, Basidiomycota)

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ACADEMIC DISSERTATION

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in Nylander-Sali (room 211),Botany Unit, Finnish Museum of Natural History (Unioninkatu 44), on November 11th, 2016, at 12:00

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ISBN 978-951-51-2663-4 (paperback)
ISBN 978-951-51-2664-1 (PDF)
http://ethesis.helsinki.fi

Unigrafia
Helsinki, 2016

Contents

This thesis is based on the following articles:

I Spirin, V., Miettinen, O., Pennanen, J., Kotiranta, H. & Niemelä, T. 2013. *Antrodia hyalina*, a new polypore from Russia, and *A. leucaena*, new to Europe. – *Mycological Progress* 12: 53–61.

II Spirin, V., Vlasák, J., Niemelä, T. & Miettinen, O. 2013. What is *Antrodia* sensu stricto? – *Mycologia* 105 (6): 1555–1576.

III Spirin, V., Runnel, K., Vlasák, J., Miettinen, O. & Põldmaa, K. 2015. Species diversity in the *Antrodia crassa* group (Polyporales, Basidiomycota). – *Fungal Biology* 119: 1291–1310.

IV Spirin, V., Vlasák, J. & Miettinen, O. 2016. Studies in the *Antrodia serialis* group (Polyporales, Basidiomycota). – *Mycologia* (revised version submitted).

V Spirin, V., Vlasák, J., Rivoire, B., Kotiranta, H. & Miettinen, O. 2016. Hidden diversity in the *Antrodia malicola* group (Polyporales, Basidiomycota). – *Mycological Progress* 15 (51): 1–12.

The corresponding Roman numerals are used to refer to these articles throughout the thesis. Main contributors to the articles are shown in the table below.

	I	**II**	**III**	**IV**	**V**
Original idea	VS, OM	VS	KR, VS	VS	VS
Data	VS, OM, TN	VS, JV, OM	VS, KR, JV	VS, JV	VS, JV, OM
Analyses	VS, OM	VS, OM	KR, VS	VS, JV	VS, JV
Manuscript preparation	VS, OM	VS, OM	VS, KR	VS	VS

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Abstract

This dissertation deals with the basidiomycete genus *Antrodia*, one of the largest polypore genera, which embraces over 80 species. Together with some other genera of brown-rot fungi (*Fomitopsis*, *Laetiporus*, *Postia* etc.), *Antrodia* constitutes its own lineage within the *Polyporales*, the so called antrodia clade. However, the genus in its current scope is polyphyletic and in need of further splitting into several natural genera.

The main aim of this study is to define what is the genus *Antrodia* as a monophyletic unity, and to revise species concepts in some of the most important species complexes in *Antrodia* sensu lato. In the strict sense, *Antrodia* is a small genus, with six species closely related to the genus type, *Antrodia serpens*. They are highly uniform morphologically but can be recognized based on meticulous pore and spore measurements, as well as ecological and geographic data.

Morphological and DNA data also allowed to revise species concepts within the *Antrodia crassa*, *A. serialis*, and *A. malicola* groups, belonging to the antrodia clade. All these revisions were based on type studies, studies of available herbarium material, and DNA analyses. In total, specimens of 46 *Antrodia* species were sequenced, 36 of them for the first time. Twelve new species were described, and six new combinations were proposed. Neotypes and epitypes were designated for seven species, in order to fix the current use of the species names.

Results of the present research can be applied to further taxonomic revisions of brown-rot polypores, as well as for introducing phylogenetically sound genus concepts in the antrodia clade. Re-evaluation of species concepts in the *A. crassa* group provided new data on the ecology and indicator values of some species, and therefore it can be useful for defining their status in regional Red Lists and lists of indicator species of old-growth forests.

Summary

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1. Introduction

Wood decomposers are one of the most important ecological groups of fungi. Depending on their wood-degrading characteristics, they are traditionally divided in two subgroups – brown- and white-rot fungi. Brown-rot fungi selectively consume cellulose and hemicellulose from wood and do not utilize lignin. Therefore the remaining lignin gives a brown coloration to the underlying wood. Although also found in many different orders of the *Agaricomycotina*, the majority of brown-rot fungi belong to the so-called antrodia clade (Polyporales), a group of poroid and corticioid genera separated recently on the basis of phylogenetic studies (Binder et al. 2005, 2013, Ortiz-Santana et al. 2013). However, taxonomic rank of the antrodia clade is still uncertain, and question about its monophyly has not been satisfactorily solved so far (Justo et al. 2015).

This study is focused on the genus *Antrodia* as it is traditionally outlined in the literature (Ryvarden 1991, Ryvarden & Melo 2014). In this wide sense, *Antrodia* is the largest genus of the antrodia clade and among the major genera of polypores (i.e. basidiomycetes having tubular hymenophore) as a whole. DNA-based studies of the genus carried out during the last fifteen years (Kim et al. 2001, Rajchenberg et al. 2011, Bernicchia et al. 2012, Ortiz-Santana et al. 2013) have confirmed that this group is highly heterogeneous. Nevertheless, no sound attempts have been made for splitting it into monophyletic taxa, mostly because of the presence of difficult species complexes, as well as vague boundaries between species of *Antrodia* sensu lato and representatives of other closely related and polyphyletic genera, such as *Daedalea*, *Fomitopsis* and *Postia*.

2. Objectives of this study

These preconditions defined the general scope of my thesis which deals primarily with several groups of phylogenetically related species in *Antrodia* sensu lato. Each of these groups is outlined on the basis of both morphological and DNA data, and species concepts within them are revised. In the future these species complexes may turn out to be good monophyletic genera although much sturdier evidences and wider sampling are necessary for such a far-going taxonomic novelties.

My interest in this group of fungi arouse while collecting polypores in my home area in the European part of Russia. Some specimens could not be identified with manuals which were in a common use at the time: morphological characters clearly indicated that they belonged to the genus *Antrodia* in the wide sense, but no existing species names were found. DNA sequences of these problematic collections, obtained in the University of Helsinki, showed that some of them represented an unnamed species while others belonged to *Antrodia leucaena* described some years before from China (I). At the same time, wider sampling of some *Antrodia* species prepared for that paper revealed an unexpected degree of polyphyly within the genus. This induced my attempts to understand what species are members of *Antrodia* in the strict sense, if the latter is considered a phylogenetic unit. Further research reduced the genus to six species only (from about 80 now listed under *Antrodia*), allied to the generic type, *A. serpens* (II). Thereafter, my studies were devoted to the *A. crassa* and *A. serialis* groups which are only distantly related to each other and to *Antrodia* in the strict sense. Intensive collecting in Europe, East Asia and North America, laborious microscopic work and phylogenetic analyses based on three genetic markers allowed me to establish modern

species concepts in these complexes (III, IV). Finally, taxonomy and phylogeny of the *A. malicola* group were revised, and a strong indication of ongoing speciation was detected therein (V).

The main intention of this study is to find solid grounds for the subsequent taxonomic work, in particular, for justifying a phylogenetically reliable genus division of *Antrodia* s. lato. Due to low morphological variability in this group, it is not an easy task. As shown in this study, searching stable morphological markers for species and species groups is time-consuming but in most cases not at all hopeless.

3. Material and methods

My research was conducted as a combination of two methods – morphological studies and DNA analyses. Traditional microscopic routine was used for primary identification of specimens at hand and for making measurements of anatomical structures (basidiospores, basidia and tramal hyphae). After that, morphological conclusions were tested by DNA methods, via comparison of LSU and ITS sequences in the first round, and also of *tef1* sequences if combined LSU – ITS data allowed no clear conclusions.

Species concepts presented in this study are based on my studies of type specimens (if available) or modern collections from the same geographic areas and preferably from the same hosts as they were reported to grow in original descriptions. As a rule, type specimens or their recent substitutes were sequenced (summarized in Table 1) and compared with sequences of morphologically similar specimens from different localities and / or hosts. As I believe, this allowed to avoid using older names in an ambiguous way, and to describe new species with a low risk of placing them into synonymy of already existing names.

Morphological study

Morphological study followed a standardized routine for all papers presented. Dried basidiocarps were cut in a few sections for measuring tube and context / subiculum thickness and checking their colour and consistency. The number of pores per mm (in some cases also per cm) was counted using a stereomicroscope (20 measurements per specimen made). Microscopic structures were studied with a light microscope and measured in a phase contrast illumination, with 0.1 μm subjective accuracy: for each specimen, 30 basidiospores, 20 tramal skeletal hyphae, and, in some cases, 20 fully developed basidia and 20 subicular hyphae were measured. Cotton Blue was used as a basic microscopic mountant for making measurements.

DNA study

Two regions of nuclear ribosomal DNA (nrDNA), internal transcribed spacer region (ITS) and the following large subunit coding region (LSU or 28S rDNA), are traditionally used in phylogenetic studies of the basidiomycetes. Both of them were used for this study, too. Phylogenetic relations between groups of species were proved based on LSU sequences. Except in a few cases, ITS sequences (in this study mainly ITS1, 5.8S and ITS2 regions) in all species complexes studied are highly conservative, with a fairly small number of variable positions, and therefore additional nuclear protein-coding gene translation elongation factor 1-α (*tef1*) sequences (Matheny et al. 2007) were crucial in justifying delimitation of most species.

The sequence datasets were aligned with MAFFT (Katoh et al. 2005, Katoh & Toh 2008) and manually adjusted. Bayesian inference (BI) (I, II, III) and / or Maximum Likelyhood (ML) (III, IV, V) phylogenetic analyses were conducted with aligned sequences (Ronquist et al. 2012, Stamatakis 2014).

4. Results

Results presented in Papers I – V confirm that genus *Antrodia* in its traditional scope is polyphyletic. Most species that have been addressed to it belong to other lineages within the large antrodia clade where they appear in between representatives of the morphological genera *Daedalea*, *Fomitopsis* and *Postia*. During this study, six monophyletic lineages (of possible genus rank) were studied and characterized in detail:

1) *Antrodia* s. str. (= *A. heteromorpha* group) with six species included (II). One of those species, *A. heteromorpha*, is holarctic; it inhabits mainly coniferous hosts although regularly occurs also on angiosperms. The rest of the species, including the genus type, *A. serpens*, grow on deciduous substrates (with exceptional records on conifers) and are limited to certain geographic areas with temperate to boreal climate.

2) *A. albidoides* group, so far represented by one described species from the Mediterranean and Africa (II). Superficially, *A. albidoides* looks very similar to *A. heteromorpha* and its allies but is only distantly related to them. At least one more species from Southern Africa exists in this group although it is not published yet.

3) *A. hyalina* group with a single species occurring on wood of aspen in temperate Europe (I).

4) *A. crassa* group which encompasses eleven species on coniferous hosts, from subtropical to boreal zones of the Northern Hemisphere (III). All but one species are specialists occurring preferably in old-growth forests and, in most cases, isolated from each other in geographic distribution. This group is closely related to the genus type of *Amyloporia*, *A. xantha*; however, for now I refrain from placing *A. crassa* and its kin to that genus. Two species in the group, *A. sitchensis* and *A. sordida*, possess identical ITS regions but they are recognizable due to their morphology, geography and different *tef1* sequences.

5) *A. serialis* group contains thirteen species (IV), and none of them is holarctic or polyphagous. Alongside boreal conifer-dwelling species more or less strictly connected either to spruce or to pine, there are two temperate species restricted to aspen and one to oak. Two relatives of *A. serialis* – *A. alaskana* and *A. calcitrosa* – have minimal differences in ITS sequences but their *tef1* sequences are much more dissimilar and morphological characteristics do not overlap.

6) *A. malicola* group consists of five tropical – temperate species (V). While three species possess clear differences in morphology, ITS and *tef1* sequences, and seemingly also in ecology and distribution, two other species, *A. malicola* and *A. kuzyana*, demonstrate ongoing speciation in East Asia.

Specimens of 46 *Antrodia* species were studied while preparing this dissertation, and 36 were sequenced for the first time. Of them, 41 species are accepted (Table 1). In total, twelve new species were described, and six new combinations were proposed. Neotypes and epitypes were designated for seven species, in order to fix the current use of the species names. The list of taxonomic novelties includes:

Antrodia hyalina Spirin, Miettinen & Kotiranta, sp. nova (I)
Antrodia favescens (Schwein.) Vlasák & Spirin, comb. nova (II)
Antrodia tanakai (Murrill) Spirin & Miettinen, comb. nova (II)
Antrodia cincta Spirin, Vlasák & Miettinen, sp. nova (III)
Antrodia cretacea Runnel, Spirin & Lõhmus, sp. nova (III)
Antrodia ignobilis Spirin & Vlasák, sp. nova (III)
Antrodia ladiana Spirin & Runnel, sp. nova (III)
Antrodia piceata Runnel, Spirin & Vlasák, sp. nova (III)
Antrodia pinea (B.K. Cui & Y.C. Dai) Spirin, comb. nova (III)
Antrodia alaskana (D.V. Baxter) Spirin & Vlasák, comb. nova (IV)
Antrodia angusta Spirin & Vlasák, sp. nova (IV)

Antrodia calcitrosa Spirin & Miettinen, sp. nova (IV)
Antrodia flavimontis Vlasák & Spirin, sp. nova (IV)
Antrodia morganii (Lloyd) Spirin & Vlasák, comb. nova (IV)
Antrodia serrata Vlasák & Spirin, sp. nova (IV)
Antrodia cyclopis Miettinen & Spirin, sp. nova (V)
Antrodia kuzyana (Pilát) Spirin & Vlasák, comb. nova (V)
Antrodia tuvensis Spirin, Vlasák & Kotiranta, sp. nova (V)

5. Discussion

Starting from the works of Corner (1935, 1953), hyphal structure ('hyphal system') has been regarded as one of the most profound characters for taxonomy of the higher basidiomycetes and polypores in particular. The morphology-based genus division of brown-rot polypores, prevailing in current taxonomic literature, corresponds to Corner's concept of hyphal systems as a whole: species with monomitic hyphal structure (all hyphae more or less uniform, clamped) are placed to the genus *Postia* (= *Oligoporus*), species with dimitic structure (possessing fibrous, thick-walled and non-clamped 'skeletal' hyphae alongside thin-walled and clamped ones) to *Antrodia*, and trimitic species (with branched 'binding' hyphae, in addition to two previous hyphal types) to *Fomitopsis*. A few genera of brown-rot polypores have been characterized on their basidiospore morphology (*Sarcoporia*, *Jahnoporus*), presence of peculiar cystidia (*Amylocystis, Auriporia*) or absence of clamp connections (*Laetiporus, Pycnoporellus*), but they do not change this outline too much. In general, hyphal structure is regarded to correlate with basidiocarp type and, consequently, with the life strategy of a species: monomitic taxa possess ephemeral, usually soft basidiocarps, dimitic ones have sturdier, seasonal fruitbodies, while trimitic taxa produce tough, as a rule perennial basidiocarps (Ryvarden 1991).

However, according to our current knowledge, this simplistic approach, useful for making identification keys and popular manuals, is not applicable to the phylogenetically sound taxonomy of the antrodia clade. As shown in Papers I, II, IV and V, at least three species complexes of *Antrodia* s. lato, the *A. heteromorpha* group (= the genus *Antrodia* in the strict sense), *A. serialis* group and *A. malicola* group, encompass monomitic or nearly monomitic species. It could be interpreted as a general trend in the basidiocarp evolution of these groups – as transition from completely resupinate, ephemeral, often richly fertile fructifications to effused-reflexed / sessile, persistent basidiocarps sporulating for short periods only. This subject deserves a closer look, and, at least in some cases, I cannot exclude reversals from persistent to ephemeral basidocarps, especially for species existing in areas under extreme environmental conditions where favorable season is short and, therefore, sophisticated anatomical structure is redundant.

The species-level taxonomic studies constituting a major part of my dissertation revealed that there are no universal rules for defining species concepts and species complexes in the antrodia clade. In all the cases treated, exceptions from a general trend can be found, and there are neither universal morphological features shared by each species included in the given group nor markers valid for each case of introducing new species. In other words, both species groups and species proper are recognizable due to sets of characters – morphological (at the supraspecific level) and, additionally, ecological and geographic (for species recognition). Revealing these characters is a matter of intensive collecting in different geographic areas and elaborate microscopic work and DNA studies.

Acknowledgements

First of all, I would like to thank my supervisors, Tuomo Niemelä and Otto Miettinen (University of Helsinki) for sharing ideas, time and specimens with me, and for providing their friendly support during difficult periods of my life. Josef Vlasák (České Budějovice, Czech Republic) generously sent excellent collections from his personal herbarium and made an essential part of the sequencing work. I am very grateful to Karl-Henrik Larsson and Jenni Nordén (University of Oslo, Norway) for offering me job opportunities which helped to continue my research. A revision of the highly obscure *Antrodia crassa* group was possible due to my collaboration with Kadri Runnel and Kadri Põldmaa (University of Tartu, Estonia) who patiently sequenced endless amounts of specimens I sent to them. Heikki Kotiranta (Helsinki), Leif Ryvarden (Oslo) and Yu-Cheng Dai (Beijing) kindly provided me with important collections, and the staff of the Finnish Museum of Natural History with working place and facilities. Brian Milakovsky (Vladivostok, Russia) and Igor Glushkov (Moscow, Russia) arranged my field work in Russian Far East. My collecting trips in the USA and Canada were supported by Chancellor's travel grants from the University of Helsinki.

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Table 1

Species described, reintroduced or treated in this study

Species	Place of origin; host as indicated in the protologue	Holotype or lectotype available	Recent material sequenced	Current status
**A. alaskana* (D.V. Baxter) Spirin & Vlasák (IV)	Alaska; *Picea*	+	several specimens from the US North-West sequenced	accepted
**A. albida* (Fr.) Donk (II)	Sweden; *Betula*	neotype selected	several specimens from Fennoscandia sequenced	synonym of *A. heteromorpha*
**A. albidoides* David & Dequatre (II)	France; *Phyllirea*	+	several recent specimens from southern France sequenced	accepted
**A. angusta* Spirin & Vlasák (IV)	Russian Far East; *Picea*	+	holotype sequenced	accepted
**A. bondartsevae* Spirin (I)	European part of Russia; *Tilia*	+	holotype sequenced	accepted
**A. calcitrosa* Spirin & Miettinen (IV)	Washington; *Picea*	+	holotype sequenced	accepted
**A. cincta* Spirin, Vlasák & Miettinen (III)	Massachusetts; *Pinus*	+	holotype sequenced	accepted
A. crassa (P. Karst.) Ryvarden (III)	Finland; *Pinus*	+	several recent specimens from Finland sequenced	accepted
**A. cretacea* Runnel, Spirin & Lõhmus (III)	Estonia; *Picea*	+	holotype sequenced	accepted
**A. cyclopis* Miettinen & Spirin (V)	Papua; angiosperm	+	holotype sequenced	accepted
A. favescens (Schwein.) Vlasák & Spirin (II)	Pennsylvania; angiosperm	+	several specimens from US sequenced	accepted
**A. ferox* (Long & D.V. Baxter) Gilb. & Ryvarden (III)	Arizona; *Juniperus*	+	recent specimen from Arizona sequenced	accepted
**A. flavimontis* Spirin & Vlasák (IV)	American North-West; *Pinus*	+	holotype sequenced	accepted
A. heteromorpha (Fr.) Donk (II)	Sweden; *Pinus*	neotype selected	several specimens from Fennoscandia sequenced	accepted
**A. hyalina* Spirin, Miettinen & Kotir. (I)	European part of Russia; *Populus*	+	holotype sequenced	accepted
**A. ignobilis* Spirin & Vlasák (III)	Arizona; *Pinus*	+	holotype sequenced	accepted
**A. infirma* Renvall & Niemelä (I, IV)	Finland; *Pinus*	+	several recent specimens from North Europe sequenced	accepted

Table 1 (continuation)

A. kmetii Vlasák (IV)	Slovakia; *Abies*	+	holotype sequenced	accepted
**A. kuzyana* (Pilát) Spirin & Vlasák (V)	Ukraine; *Fagus*	+	epitype, as well as several specimens from Central Europe sequenced	accepted
**A. ladiana* Spirin & Runnel (III)	California; *Pinus*	+	holotype sequenced	accepted
**A. leucaena* Y.C. Dai & Niemelä (I, IV)	China; *Populus*	+	holotype sequenced	accepted
**A. macra* (Sommerf.) Niemelä (I, II)	Norway; *Populus*	+	epitype, as well as several specimens from Fennoscandia sequenced	accepted
**A. macrospora* Bernicchia & De Dom. (II)	Italy; *Phyllyrea*	+	several recent specimens from Italy sequenced	synonym of *A. albidoides*
A. malicola (Berk. & M.A. Curtis) Donk (V)	US North-East; *Malus*	+	epitype, as well as several specimens from US sequenced	accepted
**A. mappa* (Overh. & J. Lowe) Miettinen & Vlasák (II)	British Columbia; *Thuja*	+	recent specimen from US sequenced	accepted
**A. mellita* Niemelä & Penttilä (II)	Finland; *Populus*	+	several recent specimens from Fennoscandia sequenced	accepted
A. minuta Spirin (I, V)	European part of Russia; *Populus*	+	several recent specimens from *locus classicus* sequenced	accepted
A. morganii (Lloyd) Spirin & Vlasák (IV)	Ohio; *Populus*	+	several recent specimens from US and Canada sequenced	accepted
**A. piceata* Runnel, Spirin & Vlasák (III)	Czech Republic; *Picea*	+	holotype sequenced	accepted
A. pinea (B.K. Cui & Y.C. Dai) Spirin (III)	China; *Pinus*	+	holotype sequenced	accepted
**A. pini-cubensis* Vampola, Kotlaba & Pouzar (III)	Cuba; *Pinus*	+	recent specimen from Florida sequenced	accepted
**A. primaeva* Renvall & Niemelä (I, IV)	Finland; *Pinus*	+	several recent specimens from North Europe sequenced	accepted
**A. pulverulenta* Rivoire (I)	France; *Sorbus*	+	paratype sequenced	accepted
**A. pulvinascens* (Pilát) Niemelä (I)	Sweden; *Salix*	+	recent specimen from Sweden sequenced	accepted
A. serialis (Fr.) Donk (I, IV)	Sweden; *Pinus*	neotype selected	neotype sequenced	accepted
A. serialiformis Kout & Vlasák (IV)	Pennsylvania; *Quercus*	+	holotype sequenced	accepted

Table 1 (continuation)

**A. serpens* (Fr.) Donk (II)	southern Sweden; *Ligustrum*	neotype selected by Niemelä & Ryvarden (1975)	epitype, as well as many other specimens from Central Europe sequenced	accepted
**A. serrata* Vlasák & Spirin (IV)	New Hampshire; *Picea*	+	holotype sequenced	accepted
**A. sitchensis* (D.V. Baxter) Gilb. & Ryvarden (III)	Alaska; *Picea*	+	several specimens from the US North-West sequenced	accepted
**A. sordida* Ryvarden & Gilb. (III)	New Hampshire; *Picea*	+	recent specimens from the US North-East sequenced	accepted
**A. subalbidoides* David & Dequatre (II)	France; *Phyllirea*	+	several specimens from southern France sequenced	synonym of *A. albidoides*
**A. submalicola* David & Dequatre (V)	France; *Populus*	+	several specimens from France sequenced	synonym of *A. kuzyana*
**A. tanakai* (Murrill) Spirin & Miettinen (II)	Japan; *Cryptomeria*	+	recent collections from East Asia sequenced	accepted
**A. tuvensis* Spirin, Vlasák & Kotir. (V)	Central Siberia; *Populus*	+	holotype sequenced	accepted
A. variiformis (Peck) Donk (IV)	New York; *Picea*	+	recent specimens from US and Canada sequenced	accepted
**A. wangii* Y.C. Dai & H.S. Yuan (I)	China; *Prunus*	+	isotype and paratype sequenced	synonym of *A. bondartsevae*

Species sequenced for the first time in this study are marked by asterisk (*).